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THE WANDERING TAPETAL NUCLEI OF ARISAEMA

F. L. PICKETT

The fact that in certain of the higher plants the walls of the tapetal cells break down and allow the nuclei and cytoplasm to "wander" among the developing microspores has been repeatedly noted. In the recent paper on wandering tapetal nuclei, Juel (1915) has carefully

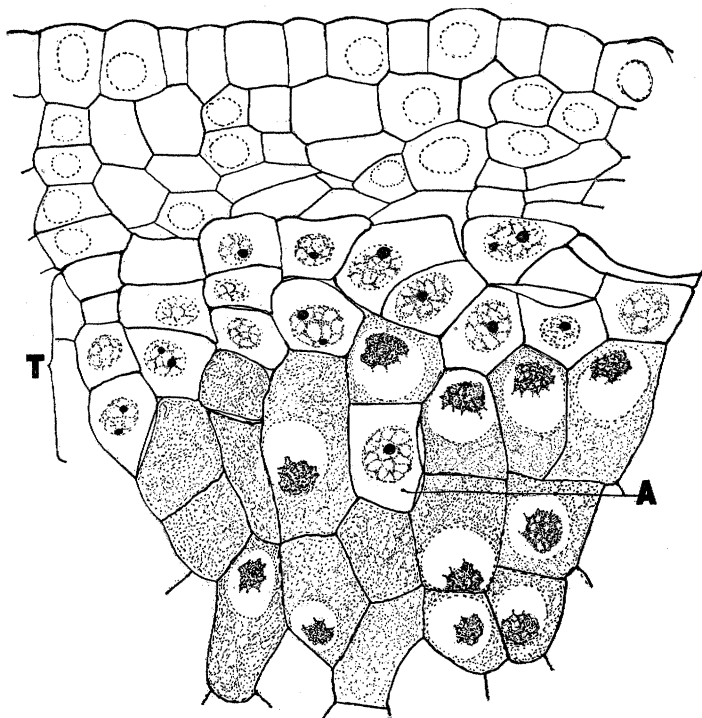


FIG. 1. Section of anther showing pollen mother-cell nuclei in synapsis and the tapetal cells, *T*, with the first indication of separation. A single sterile cell is shown at *A* surrounded by sporogenous cells. $\times 280$.

reviewed the findings of earlier workers and made important criticisms upon their reports. The great advance in technical methods has made it advisable to go carefully over the ground covered by Strasburger

and others. This Juel has done quite thoroughly, and in doing so has added much to our knowledge of the behavior of the tapetal cells. The wide range of plants in which the wandering nuclei have been found seems to indicate that much more time may well be spent in observation along this line.

Within the past year the writer (Pickett, 1915) reported the

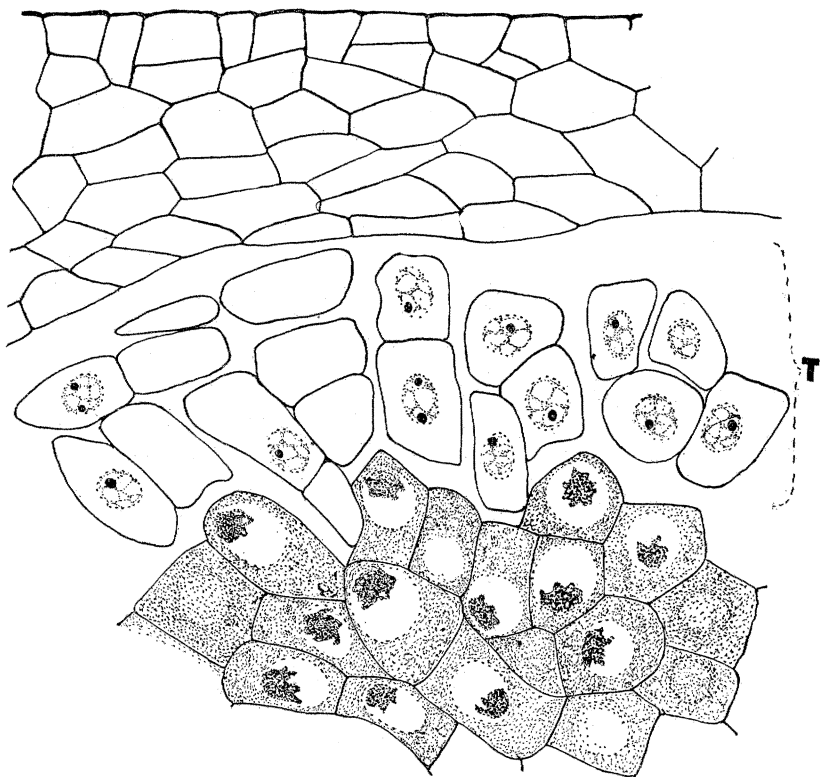


FIG. 2. A section of an anther in which the tapetal cells, T, have almost entirely separated. $\times 280$.

occurrence of wandering tapetal nuclei in *Arisaema triphyllum* (L.) Schott. The work of Juel which appeared while the writer's paper was in the publisher's hands, has made it seem advisable to go over the *Arisaema triphyllum* material again and make a fuller report. At the same time a study of *Arisaema Dracontium* (L.) Schott. has

been made, and the reports concerning the two species are here presented together.

Material for the study was collected in Indiana in 1914 and 1915. That most used was fixed in chrom-acetic acid (chromic acid 1 gm.,

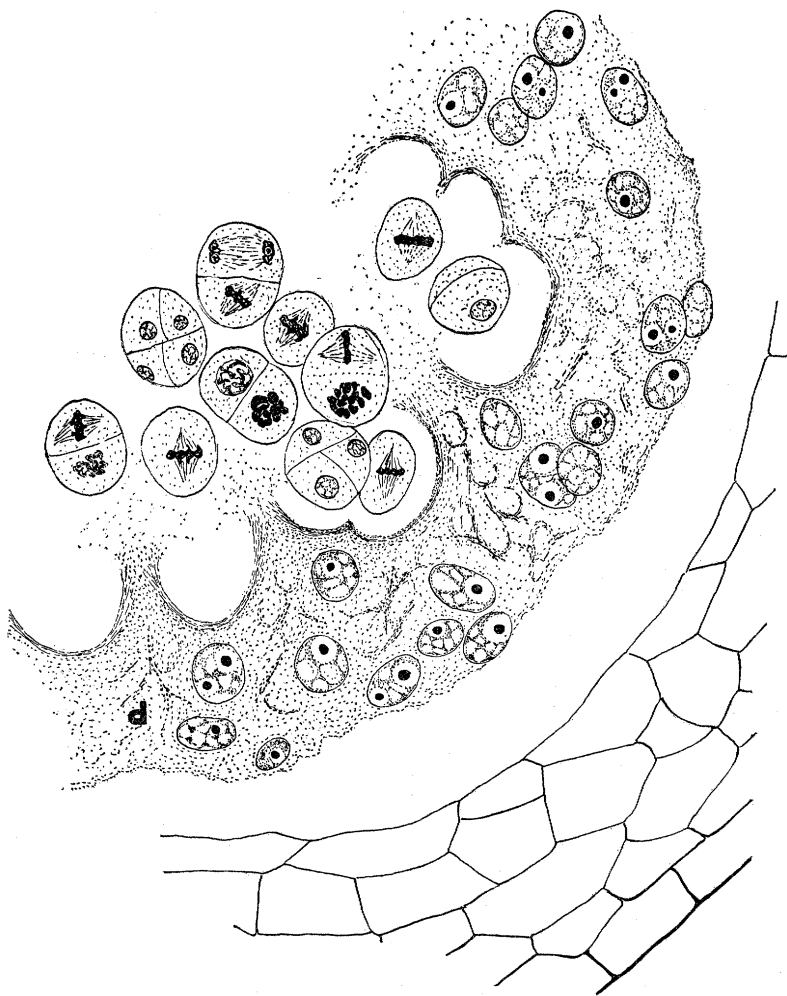


FIG. 3. Section of anther showing the periplasm, *P*, composed of the mixed masses of protoplasm from the tapetal cells and carrying their nuclei. The protoplasmic mass has not yet spread through the spaces between the dividing pollen mother-cells nor filled the anther cavity. $\times 280$.

acetic acid 1 cc., water 99 cc.). Other fixing agents were used for check material but without giving any differences with respect to the points under consideration. After the usual infiltration and imbedding in paraffin the material was sectioned $5-8\ \mu$ in thickness, and finally stained in Haidenhain's iron-alum haematoxylin, in a similar stain in which a 1/10 percent aqueous solution of brazilin replaced the usual

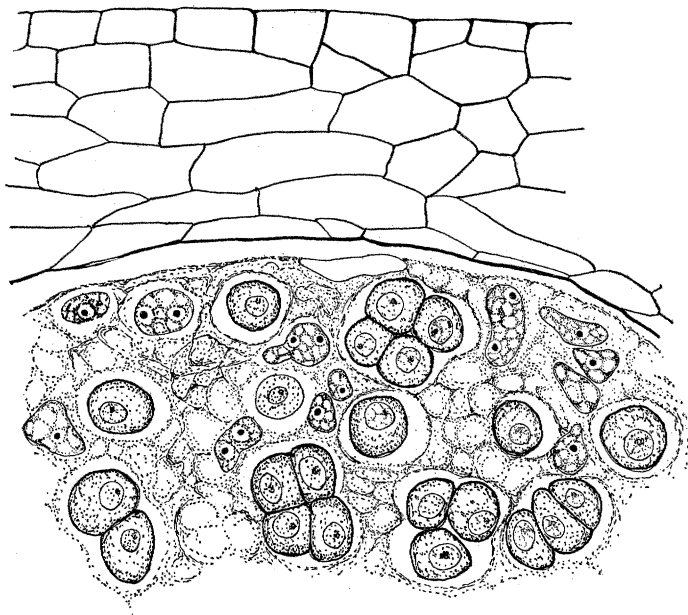


FIG. 4. A portion of an anther cavity filled with the periplasm. The tapetal nuclei have begun to change form and wander among the developing spores. $\times 280$.

$\frac{1}{2}$ percent solution of haematoxylin, and in various modifications of the triple stain, safranin-gentian violet-orange G. The best differentiation was obtained by the use of clove oil solutions of both the gentian violet and orange G as suggested in the *Annals of Botany* (29: 471-472. 1915). By the use of this stain it was always easy to differentiate the tapetal nuclei in the periplasm and to make out the smallest details of their structure. The brazilin was found of value also in the study of details of nuclear structure. A clove oil solution of "Licht-Grün" used after the triple stain above mentioned or after the Haidenhain's haematoxylin was found useful in distinguishing

between the cells of the anther wall, whose cellulose stained readily and strongly, and the tapetal cells whose walls were but lightly stained if at all.

The conditions and phenomena connected with the tapetum in the two species of *Arisaema* were found to be almost identical, so this report is made with primary reference to *A. triphyllum*. The drawings have all been made from preparations of material of that species.

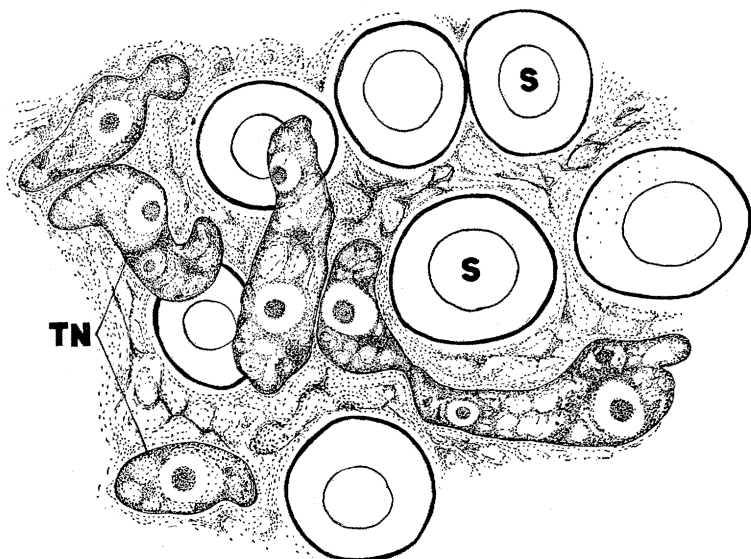


FIG. 5. A small portion of an anther cavity showing various forms of tapetal nuclei, *TN*, among developing pollen spores, *S*. $\times 1400$.

These have been carefully checked and the development of the microspores has been carefully compared with material of *A. Dracontium*. The photomicrographs in plate XX were taken from preparations of the latter species.

A section of an anther, made just before the beginning of the heterotypic division of the pollen mother-cell nuclei, shows its wall composed of a single layer of epidermal cells, and, in its thinnest part, a single row of sterile cells which later elongate radially and become thick walled. Within these two tissues there is a third, the tapetum, from two to four cells thick. The drawings have been made from portions of sections which show clearly the relation of the tapetum to

the sporogenous tissue regardless of the part of the anther wall included. The tapetal cells are clearly differentiated from those of the anther wall by their denser cytoplasm and larger nuclei. After the last vegetative division of the sporogenous cells, the tapetal cells may be distinguished, although less easily, from the pollen mother-cells by their more vacuolate cytoplasm and by peculiarities of nuclear structure. Nuclei of pollen mother-cells show the finely divided

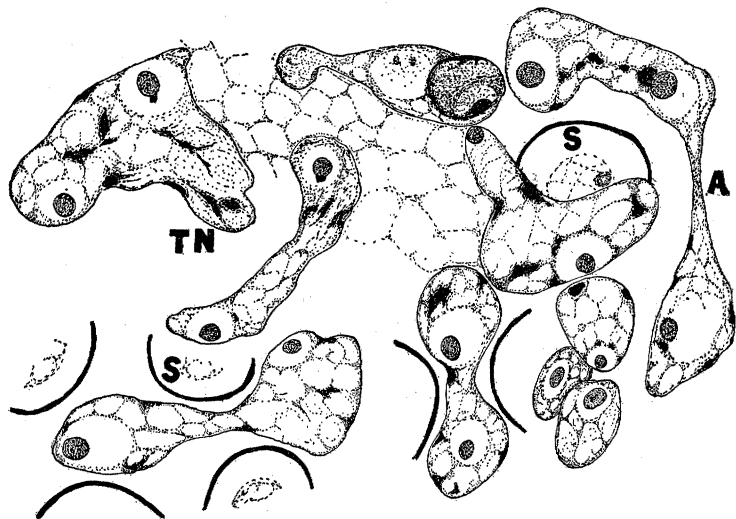


FIG. 6. A group of almost mature pollen spores, *S*, and tapetal nuclei, *TN*, the latter showing the chromatin masses characteristic of late stages. The smaller and more regular nuclei represent those with lessened activity. The nucleus at *A* suggests simple division. These nuclei are from different parts of one anther section; only enough portions of pollen spores are shown to indicate relative size and position. $\times 1400$.

chromatin and delicate linin network typical of such nuclei, while the tapetal nuclei show larger and more irregular masses of chromatin (text figure 7). With the appearance of the close synaptic ball in the nucleus of the pollen mother-cell, the typical resting nucleus serves to mark each tapetal cell even when such a cell is, as occasionally found, entirely surrounded by sporogenous cells (figure 1A).

When the tissues are first differentiated the tapetal cells are closely packed together and show distinct walls and well vacuolated cytoplasm. As the sporangial cavity enlarges through the extension of

its wall cells the tapetal cells show a tendency to pull apart and round up (text figures 1 and 2). This separation seems to indicate that normal extension of these cells has ceased and the continued enlargement of the cavity has left them without external pressure, for measurements of the cells at this time compared with similar measurements made before their separation shows no appreciable shrinkage. At this time the middle lamella has entirely disappeared and in a short time the cells, rounded up and floating in the cell sap of the sporangial

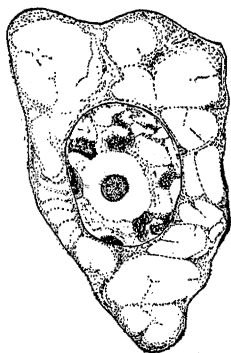


FIG. 7.

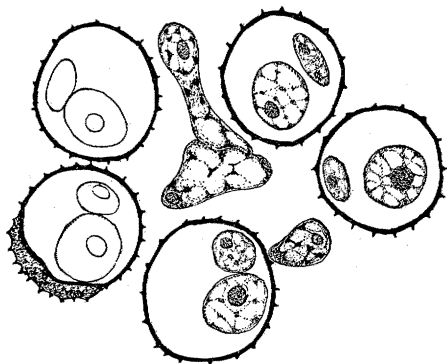


FIG. 8.

FIG. 7. A normal tapetal cell before the disappearance of the wall, showing the highly vacuolate cytoplasm, and characteristic nuclear structure. $\times 1400$.

FIG. 8. Almost mature pollen grains and a few persistent tapetal nuclei. $\times 1000$.

cavity, lose through hydrolization and solution all of their remaining cell walls. When the heterotypic division is completed the mass of pollen mother-cells is completely surrounded by the tapetal protoplasm and free floating nuclei (text figure 3). This mass of protoplasm immediately streams in between the dividing cells, surrounding each one and filling the entire sporangial cavity (text figure 4; plate XX, figure 1). From this time until the spores separate, the pollen mother-cells and the forming tetrads are within large, vacuole-like spaces in the tapetal protoplasm. The spreading of the protoplasm through the sporangial cavity is accompanied or immediately followed by a migration of the tapetal nuclei and their approximately equal distribution throughout the cavity. All this time the tapetal protoplasm or the periplasm of Hannig (1911) has shown a highly vacuolate structure.

It now becomes even more highly vacuolate, the spaces about the spores disappear and an actual contact between the protoplasm and the spore walls is evident in places.

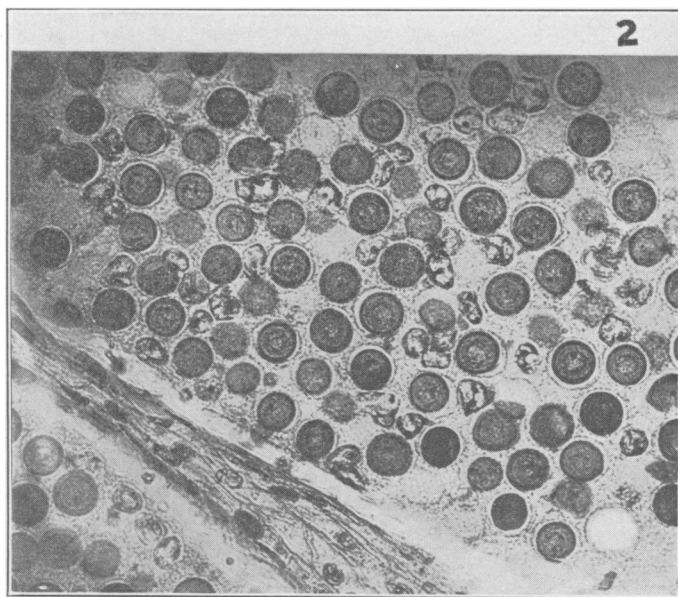
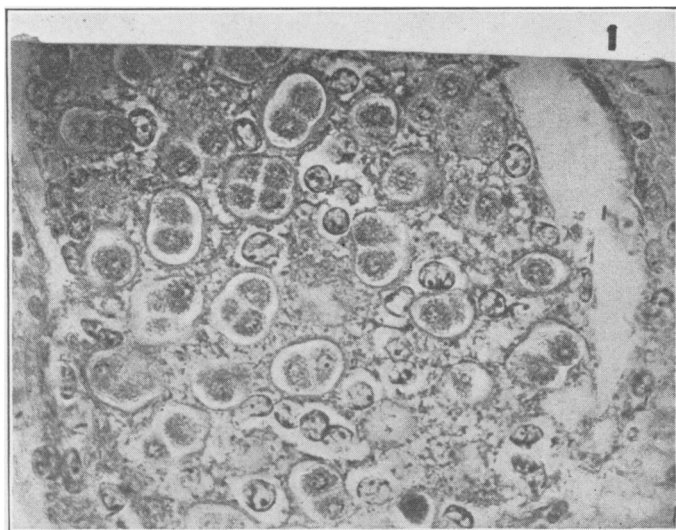
Up to the time of the general migration through the sporangial cavity, the tapetal nuclei largely retain their original form. With the movement of the protoplasm they slip between the tetrads and at the same time become slightly larger and considerably distorted in form. A marked change in nuclear structure appears. Each nucleus shows many large, irregular vacuoles and often two or more nucleoli each surrounded by a large, definite vacuole (text figure 5). They continue to increase slightly in size and show more widely varying forms, up to the time of exine formation by the pollen spores. It has been as yet impossible to demonstrate active movement on the part of these nuclei; but it is difficult to find any other explanation of the appearance of their peculiar forms so long after their first migration through the cavity. There has been found no indication of mitosis in these nuclei, and only occasional forms which seem to indicate increase in number by simple division (text figure 6, *A*) have been observed.

With the maturing of the pollen grains the protoplasm surrounding them becomes less dense, with finer strands separating the more sharply marked vacuoles (text figure 6), and finally disappears. Along with this change in the protoplasm the wandering nuclei shrink, show a decrease in general density and a gathering of the chromatin into small, almost opaque masses (text figure 6). In many cases the nuclei become more regular in form before finally shrivelling up with the loss of water when the pollen grains mature. In a few cases they retain much of their characteristic appearance until quite late (text figure 8), although most of them have lost all indications of activity before the stage of maturity indicated in this figure.

SUMMARY

The study reported at this time shows that in the development of the microsporangia of *Arisaema triphyllum* (L.) Schott. and *A. Dracontium* (L.) Schott. the tapetum is early differentiated by peculiarities of cell wall, nuclear and cytoplasmic structure.

The walls of the tapetal cells entirely disappear, allowing the several protoplasmic masses to form a periplasm spreading through the sporangial cavity.



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The tapetal nuclei for a considerable period show peculiarities of structure, and take on amoeboid forms suggestive of active migration among the developing pollen spores.

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LITERATURE

Inasmuch as the material presented above is intended merely to report observations of fact without going into any discussion of their possible bearing upon development or possible relationship of the species studied, only such literature has been cited as may help to make clear the findings reported. For a more complete bibliography see Juel's work.

Hannig. Über die Bedeutung der Periplasmodien. III. Kritische Untersuchungen über das Vorkommen und die Bedeutung von Tapeten und Periplasmodien. *Flora*, **102**: 335-382. 1911.

Juel. Untersuchungen über die Auflösung der Tapetenzellen in den Pollensäcken der Angiospermen. *Jahrb. wiss. Bot.* **56**: 337-363. 1915.

Pickett. A Contribution to Our Knowledge of *Arisaema triphyllum*. *Mem. Torrey Club.* **16**: 1-55. 1915.

EXPLANATION OF PLATE XX.

FIG. 1. A section showing the periplasm with tapetal nuclei among the spore tetrads. $\times 375$.

FIG. 2. A similar view from a section of an older anther, showing tapetal nuclei in periplasm among spores with well developed exine. $\times 375$.